TWO FORMS OF MACROPHTHALMUS JAPONICUS DE HAAN (CRUSTACEA : BRACHYURA)

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TWO FORMS OF *MACROPHTHALMUS JAPONICUS* DE HAAN (CRUSTACEA: BRACHYURA)[1)]

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With Text-figures 1–10 and Table 1

Introduction

Rhythmic motion of the cheliped, which is called "waving display," is common among the males of the ocypodid crabs, and has been studied in detail by many authors particularly for the genus *Uca*. According to Crane (1941), for example, each species of *Uca* has proved to have a definite, individual display, differing so markedly from that of every other species observed, that closely related species can be recognized at a distance merely by the manner of the display. This behavior of waving display, however, has not been reported for the species of the genus *Macrophthalmus,* except some unknown species by Tweedie (1954). Since some time ago, I have noticed that the waving display is performed in the males of *Macrophthalmus japonicus* de Haan.

This species is the type species of the subgenus *Mareotis* and is distributed widely in Japan, Korea, North China, Formosa, Singapore and Australia (Sakai, 1976), occurring commonly on the muddy substrate of littoral or estuarine area.

During my visit to Tomioka, Kumamoto Prefecture, in Kyushu in 1975, I noticed the presence of another type of waving display of this species which was different from what had been observed by me. This type of waving display was also found in two regions of Wakayama Prefecture, i.e. in the several inlets of Sirahama and in the estuary of Waka River of Wakayama. Through the examination of the specimens collected, it became evident that there existed some morphological differences between the two forms showing different patterns of waving display.

In this paper, these two forms are treated with regards to waving display, morphological characteristics and habitat. Adaptive significances of different waving display and several morphological characters of these two forms are also suggested from the ecological point of view.

I am grateful to members of the staff of the Seto Marine Biological Laboratory for their encouragements and advices given to me during the course of the study, and in particular to Dr. E. Harada for his helpful suggestions and reading the manuscript and to Mr. T. Kuwamura for his kind cooperation in collecting the specimens

1) Contributions from the Seto Marine Biological Laboratory, No. 645.

and in taking photographs of waving display. My thanks are also due to Dr. T. Sakai for giving me a chance to refer to a paper of R. S. K. Barnes by sending me the reprint.

Waving Display

Two patterns of waving display are readily distinguishable by that whether the chelipeds are unflexed or flexed at the maximum elevation in a cycle of waving.

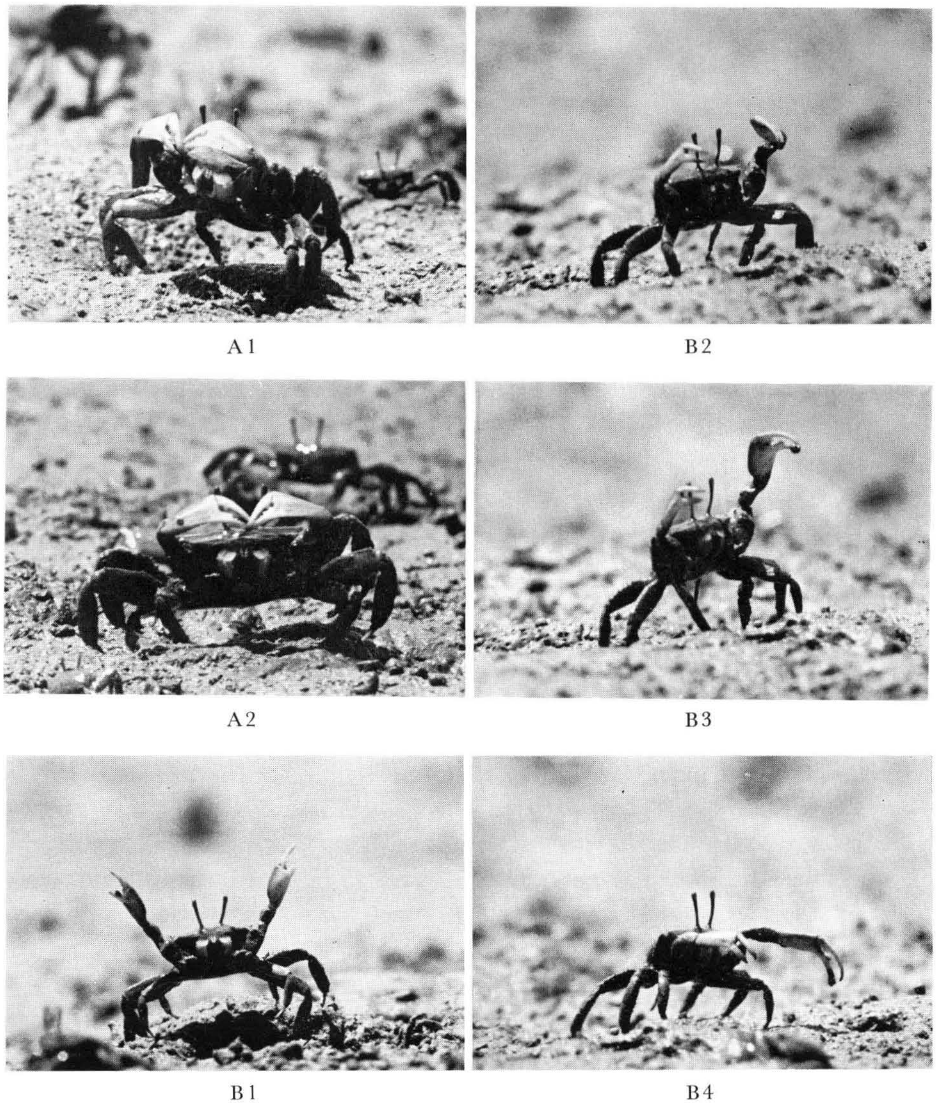

Fig. 1. Photographs showing two patterns of waving display in *Macrophthalmus japonicus* (by Mr. T. Kuwamura). A1 & A2: oblique and frontal views of vertical wave at the maximum elevation of the chelipeds; B1: frontal view of lateral wave at the maximum elevation of the chelipeds; B2-B4: the sequence of lateral wave in oblique view from the initial to the final stage.

In one pattern (Fig. 1–A), the chelipeds remain flexed throughout. At the beginning of waving they are kept in front of the buccal region, and then are raised up without unflexing. When they reach their maximum elevation above the eyes, retaining their chelae in nearly horizontal position, the body is also raised high up on the extended ambulatory legs and the 3rd ambulatory legs are also taken up off the ground. Finally the chelipeds are lowered back to the rest position, and the ambulatory legs as well.

In the other pattern (Fig. 1–B), the chelipeds which are flexed at the beginning of waving are completely unflexed, as they are raised high up. So at the maximum elevation, the chelipeds are held higher upward, but the 3rd ambulatory legs remain touching the ground, though the body is raised as in the former. Finally the chelipeds are flexed again in front of the buccal region, thus performing a more or less sweeping motion.

These two patterns are regarded to correspond to "vertical wave" and "lateral wave" respectively, into which Crane (1957) classified the basic wave patterns of fiddler crabs (genus *Uca*). These designations are adopted in the following description in this paper.

Morphological Variations

For the convenience's sake, the males showing the vertical wave and their females are referred to as Form V, and those of the lateral wave as Form L.

The waving males were captured and separated into these two forms by ascertaining their waving behavior individually. Collections were made at Yokoura of Sirahama from July to September 1976, as well as in the esturay of Waka River of Wakayama from May to July 1977 and at Sioiri of Tomioka, Kumamoto Prefecture, on 7 August, 1975. The females were captured in an area of Waka River on 1 July, 1977, where all of the waving males showed the wave of the vertical pattern, and in an area of Yokoura in Sirahama on 26 July, 1976, where the males showed solely the lateral wave. These two groups of females are regarded as Form V and Form L, respectively.

Measurements are taken as follows:

Carapace length is measured along the median line, from anterior to posterior margin.

Carapace breadth is measured between the first anterolateral angles, which is not always the widest part of the carapace.

Front breadth is measured along the anterior margin.

Propodus length of cheliped is measured from the lower end of articulation with the carpus to the tip of the immovable finger.

Manus length of cheliped is measured between the upper ends of articulation with the carpus and of that with the dactylus.

Dactylus length of cheliped is measured from the upper end of articulation with the manus to the tip of dactylus.

Manus breadth of cheliped is measured from the upper end of articulation with the dactylus to the border with the immovable finger on the lower margin.

(1) **Male**

Carapace The maximum size of the carapace in Form V is much larger than that in Form L (Fig. 6). The relative carapace length to carapace breadth in Form V is slightly larger than in Form L (Fig. 6–A1 & Fig. 7–A1). Posterolateral carapace margins of Form L are a little more convergent than in Form V, and the external orbital tooth and the second lateral tooth of Form L are directed a little more laterally than in Form V (Fig. 2). Form V shows the tendency to have a slightly broader front relative to carapace breadth than in Form L (Fig. 6–A2), but this difference is not very much distinct.

Cheliped As shown in Fig. 6–A3 and Fig. 7–A2, it is evident that Form V has a decisively shorter propodus relative to carapace breadth than Form L. But the two forms from Wakayama do not differ so widely as those from Sirahama. Namely,

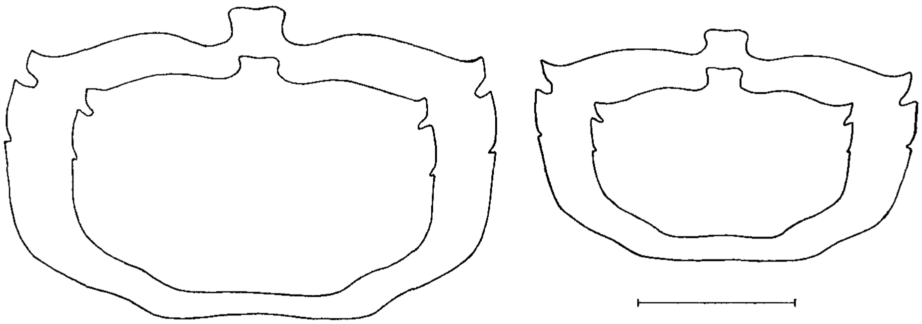

Fig. 2. Outlines of carapaces of large and small matured male specimens of Form V (left) and Form L (right). The small male specimen of Form V is chosen to be of the similar size to the large male of Form L. Scale, 1 cm.

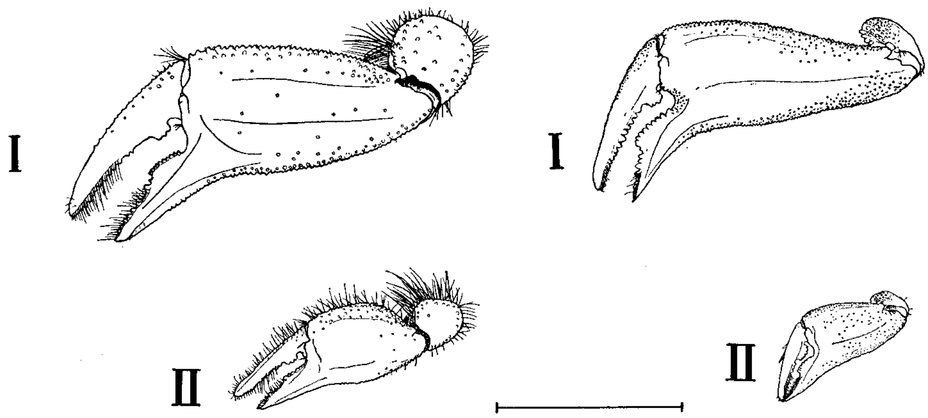

Fig. 3. The shapes of chelae of large (I) and small (II) males of Form V (left) and Form L (right). The specimens are identical with those illustrated in Fig. 2. Scale, 1 cm.

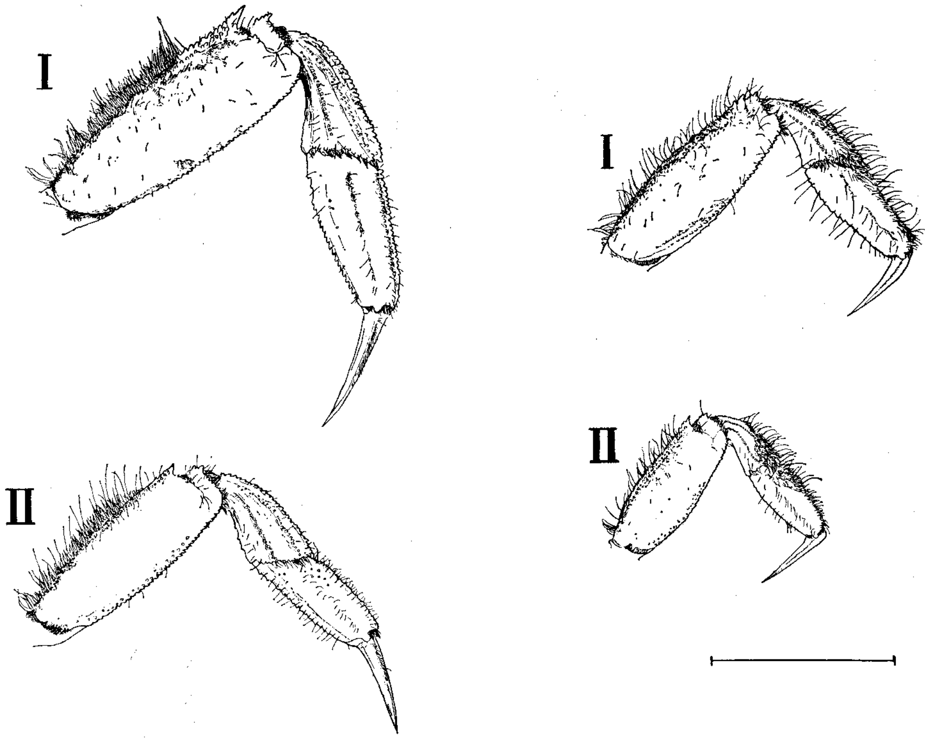

Fig. 4. The 3rd ambulatory legs of large (I) and small (II) males of Form V (left) and Form L (right). The specimens are identical with those illustrated in Fig. 2. Scale, 1 cm.

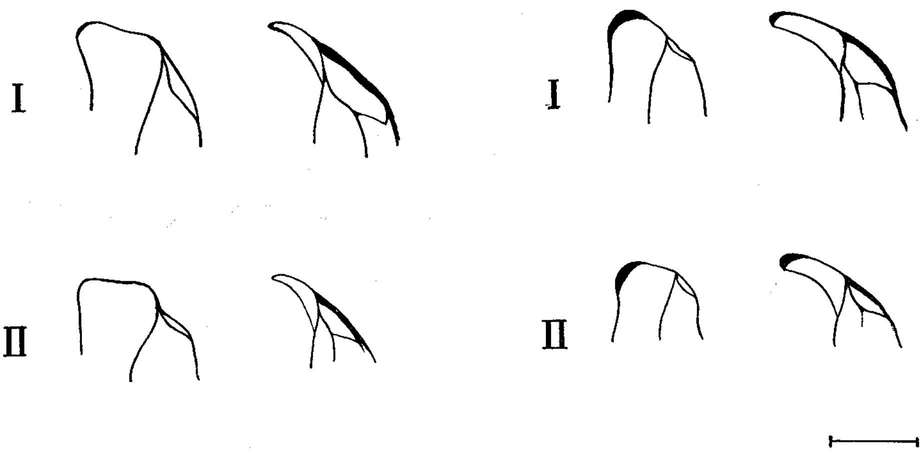

Fig. 5. Gonopod tips, setae of which have been removed, of large (I) and small (II) males of Form V (left two) and Form L (right two) in approximately lateral view (left of the two) and dorsal view (right of the two). The specimens are identical with those illustrated in Fig. 2. Scale, 0.25 mm.

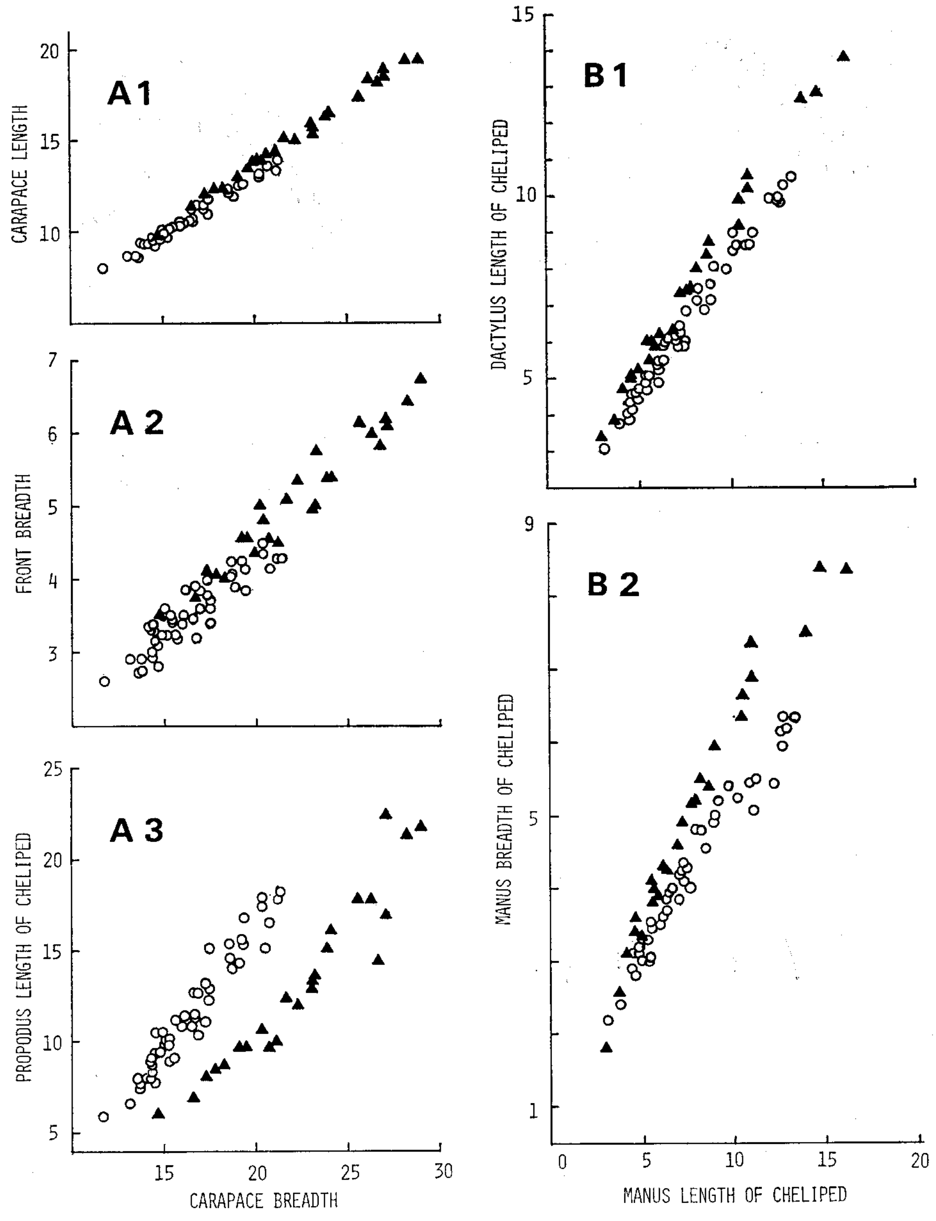

Fig. 6. Carapace length (A1), front breadth (A2), and propodus length of cheliped (A3), shown in relation to carapace breadth, and dactylus length (B1) and manus breadth (B2), shown in relation to manus length of cheliped, all in the males of the two Forms from Sirahama. The triangles represent Form V and the circles Form L. Calculated regression line formulae for carapace length are $Y=0.68X$ (0.22) for Form V and $Y=0.66X+0.01$ (0.24) for Form L, where Y is carapace length, X carapace breadth and the figures in parentheses standard errors of estimate of length (mm).

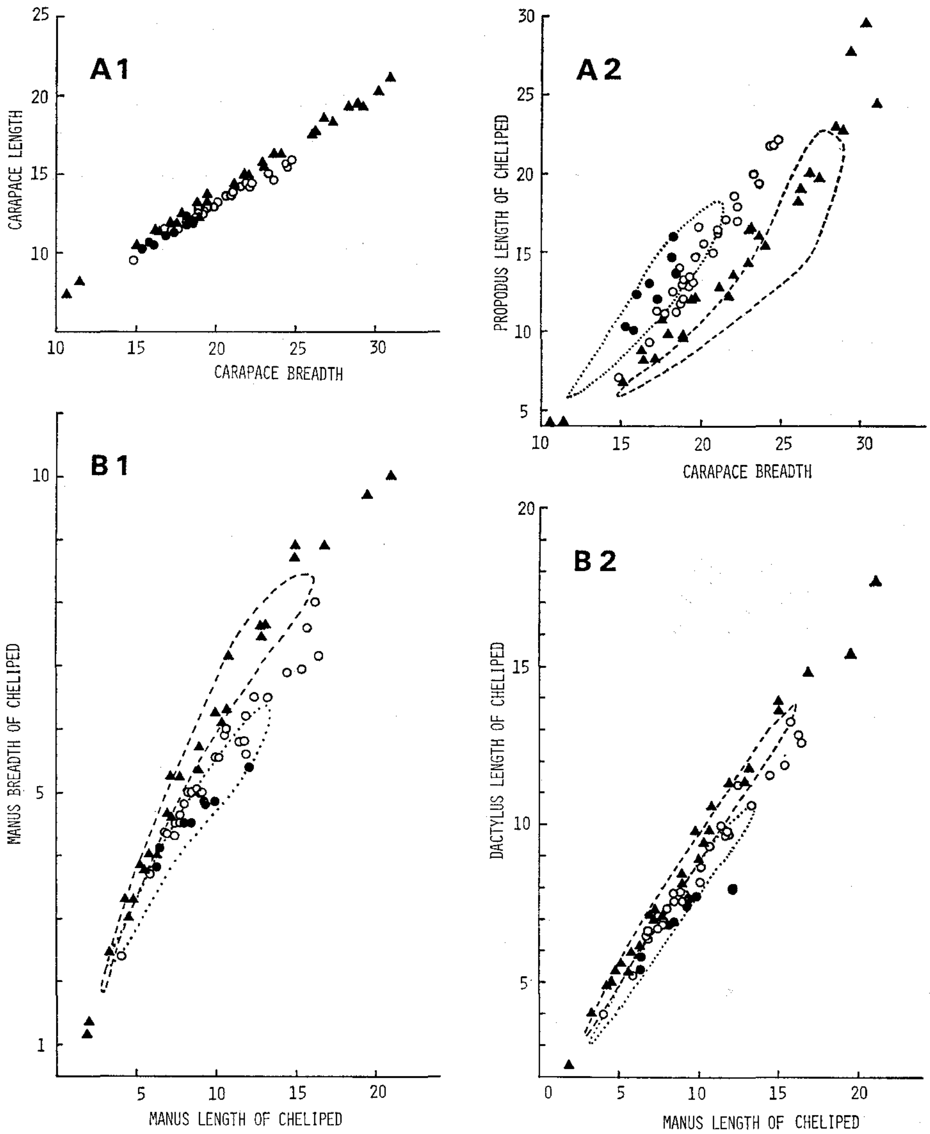

Fig. 7. Carapace length (A1) and propodus length of cheliped (A2), shown in relation to carapace breadth, and manus breadth (B1) and dactylus length (B2), shown in relation to manus length of cheliped, in the males of the two Forms from Wakayama and of Form L from Tomioka. The solid circles represent Form L from Tomioka and other symbols are same as in Fig. 6. The dotted line and the broken line indicate the ranges of Form L and of Form V from Sirahama, respectively, as shown in Fig. 6. Calculated regression line formulae for carapace length are $Y=0.68X+0.02$ (0.24) for Form V and $Y=0.65X-0.01$ (0.27) for Form L from Wakayama. Y, X and the figures in parentheses indicate the same as in Fig. 6.

Form L from Wakayama has slightly shorter chelae relative to carapace breadth than that from Sirahama, whereas Form V from Wakayama has slightly longer chelae relative to carapace breadth than that from Sirahama (Fig. 7–A2). The relative length of manus to dactylus is smaller in Form V than in Form L and the relative length of manus to its breadth is smaller as well, as are shown in Fig. 3, Figs. 6–Bl & B2, and Figs. 7–B1 & B2. But the manus of cheliped of Form L from Wakayama shows a tendency to be slightly broader than that from Sirahama (Fig. 7–B1). The wedge-shaped crenulated tooth occupying proximal half of cutting margin of the immovable finger in Form L is more conspicuous than in Form V (Fig. 3). Tubercles on the upper margin of manus in Form V are larger than in Form L (Fig. 3). Form V has a band of hair on the upper portions of the inner surfaces of dactylus, manus, and carpus, whereas in Form L there are no or very few hairs on them (Fig. 3). But those hairs of the larger specimens in Form V are less conspicuous than those of the smaller ones and some larger specimens lack them. Some smaller specimens of Form L, however, have those hairs in the same degree as the smaller ones of Form V.

Other differences between the two Forms Almost all specimens of Form L, i.e. 48 among 51 specimens examined from Sirahama and all 30 ones from Wakayama, have denser and longer hairs on the outer margins of propodus and carpus of the 3rd ambulatory legs than all 26 specimens examined of Form V from Sirahama and all 29 ones from Wakayama (Fig. 4). Moreover, upper and lower margins of meruses of the 2nd and 3rd ambulatory legs in Form L are convex at more proximal portion than in Form V (Fig. 4). The upper part of gonopod tip is, in Form V, comparatively flattened and its upper margin is almost horizontal, whereas, in Form L, the former is slightly thickened and the latter is not horizontal (Fig. 5). As for the specimens from Sirahama, these features were applied to 24 among 26 specimens examined of Form V and all 51 ones of Form L. But two specimens of Form V showed to have the features like Form L. The sternum, inner surface of the palm, and ventral surfaces of legs of Form L are pale purplish yellow, whilst those of Form V are deep yellow.

Thus it became clear that in addition to the behavioral difference there exist some remarkable structural differences between the males of the two forms. It is also clarified that the two forms differ most widely in propodus length of cheliped relative to carapace breadth among several proportional features.

(2) **Female**

Similar morphological differences are also evident in the females between the two forms in several characters stated for the males, i.e. the maximum size (Fig. 8), relative carapace length to carapace breadth (Fig. 8), outline of carapace, hairs on the outer margins of propodus and carpus of the 3rd ambulatory legs,[2] and convexity of upper and lower margins of meruses of the 2nd and 3rd ambulatory legs.

Moreover, Form V has slightly narrower abdomen than Form L (Fig. 8). Al-

2) All 24 specimens examined of Form L had marked denser and longer hairs than all 51 ones of Form V.

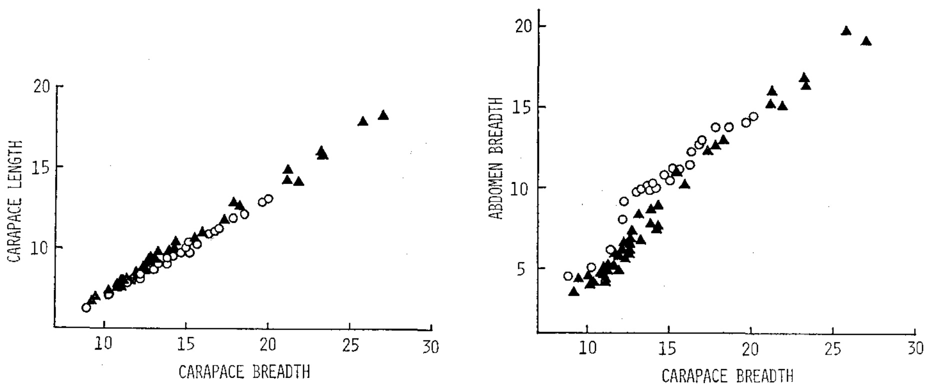

Fig. 8. Carapace length and abdomen breadth, shown in relation to carapace breadth, in the females of the two Forms. Symbols are same as in Fig. 6. Calculated regression line formulae for carapace length are Y=0.69X+0.05 (0.30) for Form V and Y=0.66X+0.02 (0.19) for Form L. Y, X and the figures in parentheses indicate the same as in Fig. 6.

though there are differences in the shape of gonopod tip in the males between the two forms, no morphological differences are noticeable in gonopore.

Habitat

The distribution of the two forms was investigated by observing the waving display in several inlets of Tanabe Bay and in the estuary of Waka River. The results are shown in Fig. 9. The occurrence of Form L is limited to the areas near the mouth of the inlets or the estuary, whilst Form V mainly inhabits the recesses of the inlets or the estuary, and also occurs less abundantly near the mouth of them, intermingling with Form L. There are no marked differences with respect to the substratum and the level between the areas inhabited by Form L and those by Form V, though the latter occasionally extend to the places of higher level (Table 1) and of less muddy substratum than the former. One of the possible environmental differences between them is that the former are flooded by more saline water for longer time than the latter. However, it was noticed that there was the tendency that in the area where the two forms occur together, Form V mainly inhabited the places of higher level than Form L, where the substratum is relatively well drained and a little firmer (Fig. 10).

Table 1. The intertidal ranges in height above datum (in cm) of the areas populated by the two Forms in the estuary of Waka River.

	From V	Form L
Number of samples	10	3
Height above datum	25–128	39–50

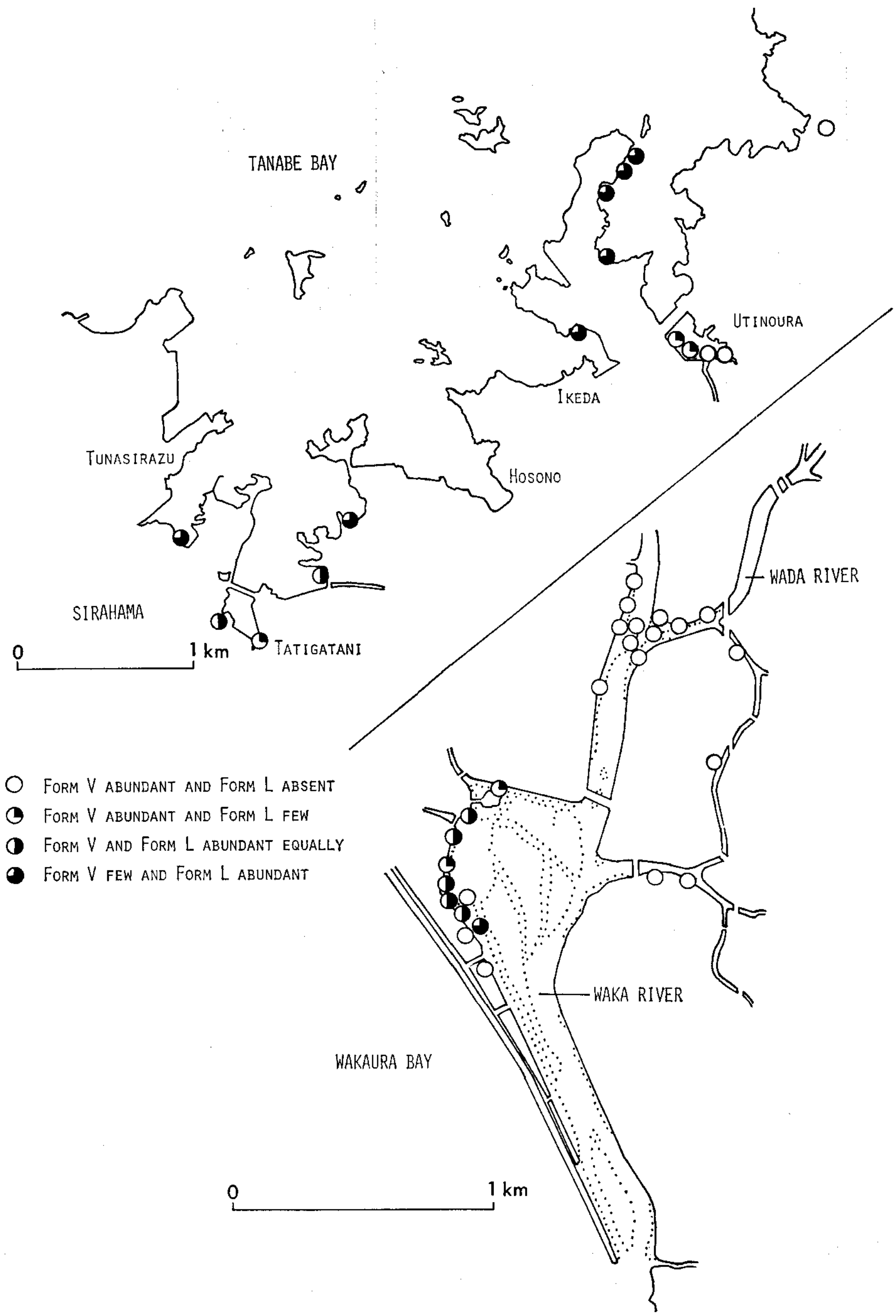

Fig. 9. Occurrence of the two Forms in some inlets of Tanabe Bay (upper) and in the estuary of Waka River of Wakayama (lower).

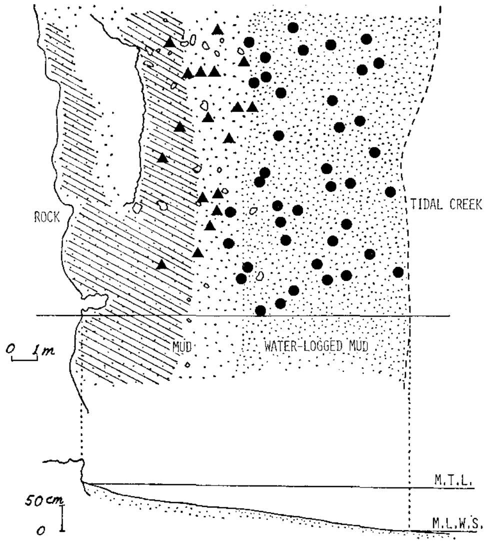

Fig. 10. An example of the distribution of the two Forms in a selected area of Yokoura of Sirahama, where both two Forms occur. The triangles indicate the males of Form V and the circles those of Form L. Shaded part shows the area inhabited by another ocypodid crab, *Ilyoplax pusillus*.

Discussion

Some Taxonomic Considerations

There has been no report so far to mention the morphological and behavioral forms of this species *Macrophthalmus japonicus,* although there are many descriptions of the species from various parts of its distributional range, i.e. Japan (Sakai, 1935, 1939, 1965, 1976), Korea (Kamita, 1941), North China (Shen, 1932), Australia (Barnes, 1967, 1970), etc. The main characters of the species described in these literatures are all applicable to the both two forms dealt with in the present paper, except the following three points: (1) the maximum sizes recorded have never been attained in Form L; (2) the feature of the tubercles on the upper margin of manus of the male cheliped in the specimens from Australia is more similar to Form V than to Form L; and (3) Australian specimens lack hair in the several parts of the male cheliped, for example, carpus, dactylus, or immovable finger, which are hairy in the present two forms.

According to Barnes (1977), the subgenus *Mareotis* contains, besides the present species, *M. japonicus,* the following twelve species: *M. abercrombiei, M. boteltobagoe, M. crinitus, M. darwinensis, M. definitus, M. depressus, M. erato, M. pacificus, M. quadratus, M. setosus, M. teschi,* and *M. tomentosus.* The morphological characteristics referred to the present two forms of *M. japonicus* have been compared with the characters of these twelve species through the descriptions of Kemp (1919), Sakai (1939) and Barnes (1966, 1967, 1970, 1971, 1977), but neither Form V nor Form L can be regarded as any of these species in these characteristics.

Thus it can be safely said that in the species which has been so far identified as *Macrophthalmus japonicus* there exist two forms which differ in several morphological and behavioral characters.

On the Sexual Isolation

In the genus *Uca* of the family Ocypodidae, waving display is generally regarded as an advertising display, and is characteristic to a male ready to court with a female and to behave aggressively toward certain other males (Crane, 1975).

In the both forms of *Macrophthalmus japonicus,* a male exhibits his waving display toward either a male or a female. When a wandering female approaches the male, he directs his wave intensively toward her and, in a successful case, leads her into his burrow, probably to complete copulation. It is also observed that a waving male approaches his neighbor male, directing his wave toward him, and consequently makes him retreat into his own burrow or, under certain conditions, leave it. Thus as in *Uca*, it seems that the waving display in the males of the both forms of *M. japonicus* serves to attract the attention of the receptive females toward themselves, as well as to threat other males.

Altevogt (1969) reported that in three sympatric species of *Uca*, i.e. *stylifera, princeps,* and *insignis,* there is an ethological isolation mechanism preventing the females of *U. insignis* and those of *U. princeps* to be carried to the burrows of the males of *U. stylifera,* which, of course, is the rule with the females of *U. stylifera.*

In *Uca*, it is generally assumed that differences in waving display and gonopod shape are apparently important means through which forms living in close sympatry avoid wasted courtship time and ineffective matings (Crane, 1975).

In the present two forms of *M. japonicus,* the patterns of waving display of them differ distinctively from each other. Although there is no evidence that the males distinguish the forms of the females in directing waving display, if the females distinguish the patterns of wave of the males and follow the males of their own form, it is quite possible that the waving display is effectively working in isolating one form from the other one. Moreover, it is probable that the structural difference in the tip of the gonopods might serve as a mean of "a mechanical isolation" which was classified as one of the isolating mechanisms by Mayr (1963).

Adaptive Significances of Morphological and Behavioral Differences between the Two Forms

Form V, the maximum size of which is much larger than that of Form L, is supposed to live in less saline situations than Form L. It is often stated for crustaceans that the smaller animals are supposed to be less tolerable to low salinity than the larger ones, because of their larger surface to volume ratio, hence high rates of water turnover (Lockwood, 1968, 1971, 1976). It seems likely that the size difference between the two forms of the present species is assoicated with the difference in salinity of their habitats.

The difference in size, on the other hand, effects the difference of conspicuousness in sighting between the two forms. However, the larger chelae relative to carapace and lateral wave in the males of smaller Form L are supposed, in a different way, to serve to make them more detectable and to be readily distinguished by the females.

Barnes (1967) proposed a hypothesis that one of the main selective pressures influencing the adaptive radiation within the genus *Macrophthalmus* is predation and this pressure has resulted in two series of structural modifications, (1) those of the ocular peduncles, and (2) those concerned with burrowing. The reduction in front breadth of the carapace and correlated increase in length of the ocular peduncles are assumed to have evolved for efficient detection of the predators. Two mechanisms of increasing the speed of burrowing are also assumed to have evolved: (1) strengthening of the pereiopods and (2) producing more slender carapace laterally. If these assumptions are extended to the two forms of the present species, the fact that smaller Form L has a slightly narrower front of the carapace and a slightly larger carapace breadth relative to its length than larger Form V may be regarded as related to effective escape from predators in the smaller form that is more vulnerable to predation. Furthermore, the marked development of the hairs on the outer margins of propodus and carpus of the 3rd ambulatory legs in Form L may also effect the increasing efficiency of burrowing.

The morphological and behavioral differences of the two forms of *M. japonicus* are thus interpreted as having in some ways adaptational meanings.

Summary

1. The presence of two forms of *Macrophthalmus japonicus* de Haan has been clarified, that differ in the waving display, morphological characters, and habitat from each other.
2. The most remarkable difference of the waving display between the two forms is that whether chelipeds are unflexed (Form L) or remains flexed (Form V) at the maximum elevation of it.
3. In the males, the two forms differ most widely in propodus length relative to carapace breadth and also distinctly in the shape of the chela and the gonopod tip. Slight difference in the abdomen breadth relative to carapace breadth is found in the females. The differences in maximum size, carapace length relative to carapace breadth, carapace outline, hairs on the outer margins of propodus and carpus of the 3rd ambulatory legs, and the shape of meruses of the 2nd and 3rd ambulatory legs are noticeable in both sexes.
4. The two forms differ also in habitat, Form L being limited to the area near the mouth of a inlet or an estuary, whereas Form V mainly inhabiting the recesses of them.
5. Adaptive significances of the different waving displays and morphological characters between the two forms were considered in relation to the habitat, the sexual isolation, and the predation pressure.

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